A NEW CASE OF PARABIOSIS AND THE "ANT GARDENS" OF BRITISH GUIANA

WILLIAM MORTON WHEELER

[Reprinted from ECOLOGY, Vol. II, No. 2, April, 1921.]

[Reprinted from ECOLOGY, Vol. II, No. 2. April, 1921.]

A NEW CASE OF PARABIOSIS AND THE "ANT GARDENS" OF BRITISH GUIANA[1]

WILLIAM MORTON WHEELER

Bussey Institution, Harvard University

The mutual hostility of ants belonging to colonies of different or even of the same species is so nearly universal, that it is surprising to find colonies belonging to different taxonomic subfamilies actually living in the same nest in a state of mutual toleration or even amity. Prof. Auguste Forel was the first to describe such an occurrence and to designate it as *parabiosis,* to distinguish it from those peculiar forms of social symbiosis, called "compound nests" and "mixed colonies," among certain Nearctic and Palearctic species. While on a trip to Colombia in 1896 he made the following observations (1898): "I often observed, for the first time in the neighborhood of Santa Martha, two species of ants belonging to different genera and even to different subfamilies, a *Dolichoderus* and a *Cremastogaster,* both of a shining black color, the former much the larger and especially broader than the latter, and of a very different form, running very generally in common files, both over the ground and on the undergrowth. The files were very long and dense, so that the ants met and elbowed one another continually.

"The two species were foraging on the bushes, the *Cremastogaster* seeking especially the plant-lice or scale insects, the *Dolichoderus* especially the juices of plants. Hence towards their terminations the files divided, each species proceeding to its own feeding ground. I finally succeeded in discovering on the trunk of a mango a large termite nest which had been appropriated by the two species of ants in question and was serving them as a habitation of a character hitherto unknown. The time for observation was unusually propitious, as each species had its sexual phases and its pupae in the nest. The latter was inhabited just as it had been abandoned by the termites, without any alterations or additions. In no part of it were the two species of ants actually mixed. Some of the corners were still occupied by the termites.

"The chambers and galleries were nearly everywhere occupied either by the *Cremastogaster* with their females, males and pupae or by the *Dolichoderus* with their females, males and pupae. Each species, therefore, had its own separate *ménage,* unlike the conditions seen in the mixed formicaries of our *Polyergus* and *Formica,* which carry on their households in common.

[1] Contributions from the Entomological Laboratory of the Bussey Institution, Harvard University, No. 175.

"But all the chambers and galleries occupied by one species opened freely into those occupied by the other and the apartments of each were intertwined indifferently. Instead of one species having appropriated one, the other the adjacent portion of the nest, they interdigitated from end to end in such wise that there was not a fragment of the nest the size of an egg that did not contain both species. The whole nest was four or five decimeters in diameter. This case is therefore very different from that of the double or compound nests of Europe, where two or more hostile species sometimes have interlacing but not intercommunicating galleries.

"We are concerned with a peaceful association for the purposes of lodging and forming files, but without mixing or a common *ménage, i.e.,* with an independent life of the two species side by side. Hence 'parabiosis,' to give it a name, which seems to me applicable to such a type of association of the two species, though very frequent, is not constant. I have also found the nest of each species in isolation, *i.e.,* apart from the other.

"Nature seems sometimes to produce associations analogous to the one here described, as *e.g.,* that of the carrion crow and hooded crow (*Corvus cornix* and *Corvus* corone) both here in Switzerland and in the north, but in this case parabiosis is less accentuated and is restricted to flocking and flying together."[2]

Later, in his taxonomic studies on neotropical ants, Forel described the two ants observed in Colombia as *Crematogaster limata* Smith subsp. *parabiotica* Forel (1904), and *Dolichoderus debilis* Emery subsp. *parabiotica* Forel (1912). The latter is now assigned to the subgenus *Monacis* in Emery's revision of the *Dolichoderinae* in the "Genera Insectorum" (1912).

In the winter of 1911–12, while collecting ants in Central America, I was able to confirm Forel's observations on the very same species. Apart from a brief reference in a paper on the Acacia-ants (1912, p. 126) my observations have not been published. I therefore subjoin the pertinent paragraphs from my notebooks written in Panama and Guatemala:

Ancon, Panama, Nov. 10, 1911.—Found a flourishing colony of *Dolichoderus* and one of *Crematogaster* living in parabosis. The nest was in single colony and without the slightest display of mutual hostility. The galleries were slender and ran lengthwise mostly. Though interwoven and more or less inosculating throughout, each gallery contained ants, larvae and pupae of only one species. The nest was disturbed and the ants kept running about in the galleries and on the bark of the tree as if forming a a strip of deadwood about 14 inches long in the cleft of a living tree. The

[2] An even more striking example is that of our common tent-caterpillar (*Malacosoma americana*) and the imported gypsy-moth caterpillar (*Lymantria dispar*). During late May partly grown individuals of the latter species are often seen peacefully nestling among the tent-caterpillars in their silken webs. This association is the more interesting because it has originated in Massachusetts within the past fifty years.

Dolichoderus worker when annoyed has a singular habit of turning its gaster upward and to one side.

Gatun, Panama, Nov. 11, 1911.—Two nests containing colonies of the black *Dolichoderus* and *Crematogaster,* very similar to the one observed at Ancon, were found in the dead wood of a couple of large tree-trunks.

Las Sabanas, Panama, Nov. 12, 1911.—A *Dolichoderus* and *Crematogaster* nest (parabiotic) was found in an abandoned termitarium in a fence post. The *Dolichoderus* were few in number compared with the *Crematogaster.*

Same locality, Nov. 17, 1911.—*Dolichoderus* and *Crematogaster* found living in parabiosis in a termite nest in a fence post still containing a few termites. The upper part of the post, for a distance of about a foot, was occupied almost exclusively by *Dolichoderus,* with males and winged females, the adjacent portion almost exclusively to *Crematogaster.* Both species were foraging in common files on the surrounding vegetation.

Tabogilla Island, Bay of Panama, Nov. 19, 1911.—A very populous parabiotic nest of *Dolichoderus* and *Crematogaster* was detected in a dead palm trunk that was still standing. Both species were about equally abundant and thier galleries about equally intermingled. There were many winged females of the *Dolichoderus.* Both species were foraging, some of the files consisting of both, others of only one of the species.

Escuintla, Guatemala, Dec. 29, 1911.—Found a nest of the small black *Dolichoderus* by itself in a fence post. The workers were attending Coccids (*Lecanium*) on the young twigs of a tree near by.

Same locality, Dec. 30, 1911.—Found a rather large parabotic nest of *Dolichoderus* and *Crematogaster* in a fence post, 3½ feet long by 3 inches in diameter. Workers of the two species were present in about equal numbers, but had no brood. They moved about together, without signs of hostility, through the intercommunicating burrows which had evidently been made by termites.

Patulul, Guatemala, Jan. 6, 1912.—A parabiotic nest of *Dolichoderus* and *Crematogaster.* Both species were attending small herds of membracids on the terminal twigs of a bush. This nest was in the rotten base of a tree but so inaccessible that I was unable to determine the arrangement of its galleries and their contents.

Same locality and date.—Two nests of *Dolichoderus* and *Crematogaster,* each in a rotten branch, scarcely more than an inch in diameter. In both cases the basal portion of the branch was occupied mainly by the *Dolichoderus* and their brood, the more distal portion mainly by the *Crematogaster* and their brood.

Same locality and date.—A large colony of the *Dolichoderus* was found in the decayed base of a living tree, but there were no *Crematogaster* in the vicinity. The nest contained many winged females.

According to Forel (1912), Christophersen has also observed the parabiosis of *D. parabioticus* and *C. parabiotica* in Panama.

In my paper on the Central American Acacia ants (1913) I described another case as one of parabiosis, namely, that of *Camponotus planatus* Roger and *Pseudomyrma belti* Emery var. *fulvescens* Emery, which often live on the same tree. They forage on the nectaries of the same leaves and though not friendly are certainly not hostile to one another. In Wasmann's opinion (1915, p. 129) this is not to be regarded as a case of parabiosis "except in a broad sense, since the two species do not inhabit the same nest but different nests (thorns) on the same trees or branches." I would point out, however, that the cavity of a single pair of thorns is properly to be regarded not as a complete nest but merely as one of the chambers of a polycladic nest represented by the whole number of thorn cavities on the tree. From this point of view I believe I was justified not only in calling the association of *planatus* and *fulvescens* parabiotic but also the cases of the ants which I found many years ago nesting in Tillandsias in Mexico, Florida and the Bahamas (1901). I admit, of course, that we have here an approach to what I called the cases of "plesiobiosis," such as are exhibited by two or more hostile or indifferent species of ants when they occupy separate though intertwined galleries in the same log or under the same stone.[3]

In 1912 Mann described two very interesting cases of parabiosis which he observed in Brazil. The first was represented by *Dolichoderus* (*Monacis*) *bispinosus* Olivier and a small black *Crematogaster,* which, he informs me, was evidently *parabiotica.* Near Pará the *Dolichoderus* "lives in carton nests, built on the branches of trees, though often a colony is found in a deserted termitarium." Large nests contain this species alone, but "in young trees along the trails there were numerous small nests, four or five inches in diameter, and several of these were opened. Each contained, besides the *Dolichoderus*, a colony of small black *Crematogaster.* The smaller ants were not scattered throughout the nest, but were grouped in certain of the chambers." From the fact that the *Dolichoderus* is a fierce and pugnacious ant, Mann infers that all the advantage of the association would be on the side of the *Crematogaster* "since it shares the nest built by the other and is well protected, without apparently contributing anything in return."

The other case was observed in Matto Grosso and is described as follows: "In August, while collecting along a trail near Camp No. 41 on the Madeira-Mamore Railroad in the State of Matto Grosso, my attention was attracted to a number of small red *Dolichoderus.* They were moving excitedly about, holding the abdomen up and a little to one side, so that they

[3] In his paper of 1915 Wasmann describes a *Pseudomyrma* from thorns of *Acacia sphaerocephala* collected by Brakhoven at Tampico, Mexico, as *Ps. canescens* sp. nov. As this name is preoccupied by *Ps. canescens* Fred. Smith of Brazil (Trans. Ent. Soc. London, 1877), I suggest that the Mexican species be known as *Ps. wasmanni* nom. nov.

had a comically asymmetrical appearance. A tree by the trail had been felled, and in a fork of its branches, at what had been a height of approximately forty feet, I found the nest, an earthy structure, ovate in form, about a foot in length and eight inches in diameter. Fine roots of a plant ramified through this nest in all directions in such a manner as to make it quite firm, despite the nature of its component material. When I dug into the structure, numbers of the *Dolichoderus* rushed out. While collecting these I had a momentary glimpse of another ant, colored similarly to the *Dolichoderus* but much larger, and with long legs. It emerged from one chamber and immediately disappeared into another. Hoping to collect this, as well as all the phases of the *Dolichoderus,* I brought to the place a large quinine can, containing a piece of cotton saturated with chloroform and began to dig and throw into this fragments of the nest. Hereupon numbers of the large ants rushed out, and my hand was severely stung before I realized that two colonies of ants, one of them a stinging form, were occupying the nest. On examination, the fragments thrown into the can were seen to contain large numbers of both species, together with many larvae and pupae of each. The larger one proved to be a Ponerine, of the genus *Odontomachus.* Males and females of *Dolichoderus* were also found, but there were none of these phases of the other. But the presence of many larvae in all stages showed that the sexual forms of both species must have been present. During the two days following I revisited the nest frequently, and stirred it up. Each time both species of ant sallied out. Touching the nest lightly would bring out *Dolichoderus,* but it required a more vigorous prod to excite the other. My first examination had so disarranged the nest that I could make no close study of its structure, but was able to ascertain that the *Odontomachus* were gathered together in its deeper recesses, while the smaller species occupied the peripheral chambers and galleries. No other nest was found, nor did I again find either of the ants. This may be readily explained by the usual inaccessibility of tree tops to the collector, so failure to find more in no wise proves that the species are uncommon."

Mann adds: "The observations here recorded seem to indicate a much closer relation than that of *Dolichoderus* and *Cremastogaster,* for it is evident that both species would derive benefit from the association. In the earthy, arboreal nest of *Dolichoderus, Odontomachus* finds a condition similar to that of the ordinary nesting place of the genus, while to the other, a feeble species, the advantage in having a colony of powerful stinging ants in the same nest is obvious, provided of course that it, itself, is not molested. For the reasons stated above, I do not believe that such molestation occurs."

The two ants were described in the paper from which these passages are quoted as *Odontomachus affinis* Guérin subsp. *mayi* Mann and *Dolichoderus* (*Monacis*) *debilis* var. *rufescens* Mann, the latter being, therefore, merely a red variety of the form observed by Forel, Christophersen and

myself living in a similar relation with *Crematogaster parabiotica* in Colombia, Panama and Guatemala. I have reproduced Mann's observations in full because they show very clearly that his "nest" of *Odontomachus* and *Dolichoderus* was really an "ant-garden" of the type described and figured by Ule (1901), and as the observations I have to record relate to these same structures, a more detailed account of them will not be out of place.

While studying the Brazilian hylaea in 1900 Ule found attached to the branches of trees, in certain localities, balls of earth bristling with epiphytes in various stages of germination and growth and inhabited by colonies of ants. The densely felted rootlets of the plants kept the particles of soil together and formed the walls of the galleries and chambers occupied by the insects. The ants he took from these singular structures, which he called "ant-gardens" and later "flower-gardens" (1901, 1905, 1906) were identified by Forel (1904) as *Camponotus femoratus* Fabr. and three closely allied species of *Azteca* (*traili* Emery, *olitrix* Forel and *ulei* Forel). Ule (1905, 1906) distinguished two kinds of gardens according to their flora and the size of the ant they contained. On those tenanted by the larger species (*C. femoratus*) he collected the following plants: *Philodendron myrmecophilum* Engl., *Anthurium scolopendrinum* Kunth. var. *poiteauanum* Engl., *Streptocalyx angustifolius* Mez., *Aechmea spicata* Mart., *Peperomia nematostachya* Link, *Codonanthe uleana* Fritsch, and *Phyllocactus phyllanthus* Link. The gardens inhabited by the three small ants of the genus *Azteca* yielded *Philodendron myrmecophilum* Engl., *Nidularium myrmecophilum* Ule, *Ficus myrmecophila* Warb., *Marckea formicarum* Damm., *Ectozoma ulei* Damm., *Codonanthe formicarum* Ule and two undescribed species of Gesneriaceae. These fourteen species belonged to such different families as the Araceae, Bromeliaceae, Gesneriaceae, Moraceae, Piperaceae and Cactaceae. Notwithstanding this diversity he believed he could detect certain common peculiarities not seen in other epiphytes, notably in the structure of the roots, leaves and fruit. The fruit is usually berry-like and the seeds larger than in epiphytes growing elsewhere. He also maintains that they grow only on the ant-nests. He inferred that "the ants sow and care for these plants, which would otherwise be unable to exist, but in return enable the ants to construct arboreal nests insured against being washed away by the torrential rains and protected from the scorching rays of the sun." Ule performed some experiments which seemed to indicate that the ants may actually collect the seeds of the epiphytes. "On several occasions," he says, "I squeezed the seeds out of the berries of a *Nidularium*, another Bromeliad, related to *Portea*, and one of the Gesneriaceae onto the branches, and observed the behavior of the ants. At first they merely lapped up the juice, but on finding the seeds carried them away forthwith to the protection of their nests. On one occasion the little creatures seized the seeds at once and made off with them."

Through the kindness of Mr. William Beebe, I had an opportunity, during July, August and September, 1920, to study these ant gardens at Kartabo, British Guiana, in the neighborhood of the Tropical Laboratory of the New York Zoological Society. They were common and conspicuous objects both in the forest and jungle, not only around the laboratory, but also along the creeks on the left shore of the Cuyuni River and near the Penal Settlement. They agreed very closely with Ule's description even in their floral components. Prof. I. W. Bailey and I were able to recognize among the

FIG. 1. Three small ant-gardens on a sapling. The earthen portion of each was about the size of a large orange. (Photographed by John Teevan, Kartabo, B. G.)

plants growing out of the spherical or elliptical balls of black earth, two Gesneriaceae, an *Anthurium,* a *Peperomia* and a few Bromeliads. Some of these plants were in various stages of germination during the rains in early July, and during the first days of September we found the purplish and white flowers of the Gesneriaceae (probably species of *Streptocalyx* and *Codonanthe*), but the season for the berry-like fruits had not arrived so that it was impossible to repeat Ule's experiments.[4] The gardens were most numerous in the rather damp jungle just back of the laboratory and along

[4] In the late fall of 1920, after my return to the United States, Mr. Beebe succeeded in finding some of the ant-garden Gesneriaceae in fruit and sent me a colored sketch of a portion of one of the plants. I have inserted a line drawing of this sketch as Fig. 3. The fruit is bright red and resembles a small cherry.

the Puruni Trail. Many of them, varying from the size of a walnut or orange to that of a foot-ball, were within easy reach, but others, of greater dimensions and covered with a much denser and more luxuriant vegetation, including large Aroids and Bromeliads, were seen on the branches of tall trees 50 to 100 feet above the ground.

In British Guiana, at least, four different ants form flourishing colonies in the gardens, namely, *Camponotus* (*Myrmothrix*) *femoratus, Crematogaster limata* var. *parabiotica, Anochetus* (*Stenomyrmex*) *emarginatus* Fabr. and one or more small, black species of *Azteca,* not yet studied but apparently very closely related to if not the same as the species taken by Ule in Brazil. The *Camponotus* and *Crematogaster* are far and away the most frequent, occurring in fully 90 percent of the gardens; the Aztecas are rather sporadic and the *Anochetus* even less abundant. But what is of unusual interest, in more than 80 percent of the gardens the *Camponotus* and the *Crematogaster* live together in parabiosis!

FIG. 2. Closer view of one of the ant-gardens of Fig. 1, showing the earthen portion bearing the plants more distinctly. (Photographed by John Teevan.)

The habits of the two ants could be easily observed in a small clearing

adjoining the laboratory where all but a few trees had been cut down to make room for a cassava patch and where the vegetation at the edge of the intact jungle could be easily scrutinized. Here the *Camponotus* and *Crematogaster* were the dominant insects over an area of several acres. The former species, for its size the fiercest and most aggressive *Camponotus* of my acquaintance, makes observation in this locality anything but an unalloyed pleasure. In company with the tiny *Crematogaster* it forms long files continually descending and ascending the trees, traversing the soil and exploring the foliage. The main occupation of both species is herding Jassids and Membracids on the terminal twigs of various Melastomaceae. Leguminosae and other plants and collecting nectar from the huge extrafloral nectaries of several species of *Inga*. The pinnate leaves of these plants, unusually common along the edge of the clearing, are remarkably adapted to the visits of these and other ants. A large, saucer-shaped nectary is situated at the junction of each pair of leaflets and the alate sections of the petiole form a series of convenient bridges running the full length of the leaf. Frequently a *Crematogaster* or a *Camponotus* or one of each was seen drinking at each of the nectaries of a leaf. *Ectatomma tuberculatunt*, a large sleepy Ponerine, was also an habitual visitor to these sugar fountains. The *Crematogaster*, when alone or in small numbers, in a timid and inoffensive ant, too diminutive to be annoying, but touching a leaf or twig on which a few of the *Camponotus* are engaged in collecting their sweets is an experience to be remembered. The large workers, without a moment's hesitation, bury their mandibles in one's skin, and curving the gaster forward drench the wound with formic acid. The resulting pain is surpassed only by that inflicted by the much larger though fortunately less common *C. abdominalis*, which is also a member of the subgenus *Myrmothrix*.

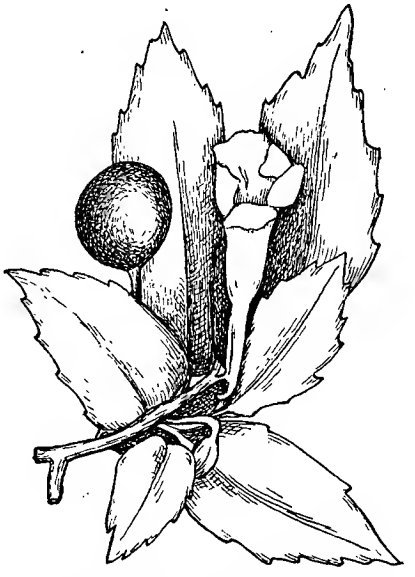

FIG. 3. Flower and berry-like fruit of an ant-garden epiphyte (Gesneriaceae), from a sketch of a specimen found by Wm. Beebe at Kartabo in November, 1920.

The common files of the *Camponotus* and *Crematogaster* are sometimes very long—more than 70 to 100 feet—and the workers of both species, intermingled, straggle along in both directions, the *Camponotus* frequently stopping for an instant to exchange antennal greetings with the *Crematogaster*.

That the two species are decidedly friendly even outside the nest is shown by the following observation. Early one morning I saw several *Camponotus* sleeping on the leaves where they had spent the night after gorging themselves with nectar. My attention was attracted to these ants because each had its head almost in contact wtih that of a *Crematogaster*. As soon as the sun rose and the air grew warmer the ants awoke and in three instances I saw a *Crematogaster* apply its tongue to the mouth of its large companion and receive a regurgitated droplet of nectar. After this early breakfast the couples separated and proceeded to the business of the day.

Within the nest the relations of the two species are peculiar. If a large ant-garden containing both species be slightly disturbed, the *Crematogaster* rush out in great numbers to attack the intruder. Further disturbance brings out some of the *Camponotus,* but not till the nest is rudely shaken or broken open do the formidable battalions of the latter rush to the surface and with keen bites and formic acid batteries reinforce the feeble efforts of the *Crematogaster*. An examination of the nest under such circumstances is as confusing as it is painful, for the chambers and galleries are full of workers of both species running about with their brood in the wildest excitement. I found that much more satisfactory results can be obtained by quickly cutting off the branch close to each end of a garden and enclosing it in a paraffine bag containing a wad of cotton soaked with chloroform, for the ants are so rapidly asphyxiated by this method that they have no time to move their brood. When a nest thus treated is bisected, all the superficial galleries and they alone are found to be stuffed with *Crematogaster* and their larvae and pupae, whereas the *Camponotus* with their larvae and cocoons occupy only the center, or core of the garden. This arrangement accounts for the successive attacks of the two species when the nest is disturbed. Since the galleries of both species open into one another the adult ants undoubtedly mingle and move about together more or less, but the broods of the two species are kept rigidly separate, so that we have really a "compound nest" and not a "mixed colony."

The percentage of parabiosis of the two species under consideration at Kartabo is so high that one is inclined to regard it as a case of mutualism in actual process of development. It is obvious that the little *Crematogaster* must find association with such a powerful and aggressive ally as the *Camponotus* very advantageous, and it would seem that the latter species must find the presence of *Crematogaster* more or less beneficial. The two species probably require different optimum nesting conditions, the *Crematogaster* and their brood a greater exposure to the heat and the air and the *Camponotus* a cooler and damper situation. This would account, perhaps, for the different parts of the garden they select as their habitations. But the association may be advantageous to both species for two other reasons: first, the combined worker population of the two colonies, merely as a matter of

numbers, as furnishing both more laborers for the construction of the nest and more warriors for defence against common enemies, such as alien ants, birds, monkeys and smaller mammals, and second, the colonies of the two species together are comparable to a single colony in which the polymorphism and therefore the physiological division of labor among the workers is extreme. The tendency to develop such types of polymorphism, which manifests itself in many phylogenetically unrelated ants (*Pheidologeton diversus, Solenopsis geminata,* many speices of *Pheidole, Camponotus, Azteca, Dorylinae,* etc.) implies an increased range of activities of a worker caste and is tantamount to increasing the efficiency of the colony as a whole. In the case under consideration the combined parabiotic colony may be said to exhibit a greatly increased range of effective worker polymorphism extending from individuals measuring only 2.3 to 2.7 mm., the length of the *Crematogaster parabiotica* workers, to those measuring 4 to 9 mm., the length of *Camponotus femoratus* workers.

A review of the various known cases of typical parabiosis recorded in this paper shows that *Crematogaster parabiotica* exhibits the most pronounced tendency to associate with other ants. It is now known to nest with three different species in different parts of its range: with *Dolichoderus parabioticus* in Colombia, Panama and Guatemala, with *D. bispinosus* in Brazil and with *Camponotus femoratus* in British Guiana, and in each instance its associate is a larger and more pugnacious species. The same conditions are exhibited by *D. rufescens* and *Odontomachus mayi.* All of these cases may be due both to a small feeble ant seeking out and profiting by the protection of a more powerful species and to the advantages accruing to both associates in forming a single large colony with increased range of worker polymorphism. The fact that in every case the pair of species living in parabiosis belong to different taxonomic subfamilies very probably prevents them from uniting their broods and fusing completely to form a mixed colony.

It is evident that the various species of *Crematogaster, Camponotus, Azteca* and *Anochetus* together with the numerous epiphytes growing on their nests constitute a peculiar biocoenose, but I fail to see that its evolution or the ethological relations of its animal and plant components have been satisfactorily elucidated by Ule. In his first paper (1901) he advances the following considerations in support of his contention that the seeds of the epiphytes are sown and the plants cared for by the ants:

"1. We are unable to believe that these ant-nests are always established where there happen to be seeds of the plants, and that such numbers of often very different seeds can find their way into the ant-nests through the agency of birds or any other animals, except ants. Then, too, the ant-gardens are often established in places where other epiphytes are never seen.

"2. My contention is supported by the fact that particular species of plants occur nowhere but in the ant-nests.

"3. We must consider also the peculiar structure of the ant-epiphytes, which are unable to grow except on an artificial accumulation of humus.

"4. Finally, experiments were performed, which show that the ants actually transport the seeds of the ant-epiphytes to the proper situations."

In his paper of 1906, written presumably some time after his return to Germany, we have this less inferential and more positive statement:

"I have established the fact that ants carry the seeds of certain plants into the crevices and crotches of trees and bushes or into earthen nests built in such places and then by bringing up more and more earth encourage the growth of the plantlets and thus secure greater volume and firmness for their construction." He also offers the following remarks on the phylogenetic development of the structures under discussion:

"Presumably the flower-garden arose from the ants occasionally establishing their nests among epiphytes, thus acquiring a more secure foundation for them. The ants then fed on the juicy berries of these epiphytes and occasionally carried their seeds into the crevices of the bark, where some of them germinated and in turn gave protection to ant-nests. But as soon as these clever little insects perceived the usefulness of the growing epiphytes, they took greater care to encourage their growth, and their cultivation became an inherited habit. The plants cultivated by the ants now adapted themselves to the conditions or became modified and in part survived only in the flower-gardens. *Unquestionably, the ants, when founding new nests, carry seeds into them from the old nests,* a fact that would be most easily explained in the case of *Camponotus femoratus,* which often occurs in great numbers in the same locality. At times of flood the flower-gardens would be distributed now and then by fallen and floating trees. In the single gardens which occur more sporadically, as is more frequently the case with those of *Azteca,* the plants could reach their destination only if their seeds were carried long distances by the ants. It is a striking fact that certain species of ant epiphytes occur again and again as single specimens in such widely separated localities. Since the ants have selected and cultivated for their nests plants which then became dependent on their activities, it is *demonstrated, that these animals are able to adapt themselves to the plants, to modify their structure and to take advantage of their peculiarities.*"

I have cited these passages because they may be regarded as a classical example of the uncritical mixtures of observation, inference, assertion and speculation, which abound in the work of observers in the tropics and constitute the only foundation on which some of the closet naturalists of Europe and the United States have been building their specious hypotheses. Although, as above stated, I was unable to repeat Ule's experiments with the epiphyte seeds, owing to the unfavorable season, the British Guiana ant-gardens are so similar to those observed by Ule in Brazil, that I feel justified in offering the following comments:

1. The frequent parabiosis of *Crematogaster parabiotica* and *Camponotus femoratus* shows that Ule's distinction of gardens inhabited by large and small ants does not hold in British Guiana. Moreover, though the same plants do not occur in all gardens, no preference of certain ants for certain plants could be detected.

2. All the species of ants involved in the ant-garden biocoenose may also nest elsewhere. Even the *Camponotus* and *Crematogaster* are occasionally found nesting in very different situations, though it must be admitted that the former shows a very decided preference for the garden nest. The fact that Ule found this same insect so frequently in the same structures in Brazil, shows that there is here a very regular and intimate ethological relationship between an ant and certain epiphytes. *Anochetus emarginatus* is less frequently found in gardens than in the rotting cores of tree-trunks, stumps or branches, or accumulations of woody detritus under loose bark or the bases of palm leaves. Nevertheless, the plants growing in gardens inhabited by *Anochetus* are as abundant and of the same species as those on the nests of *C. femoratus*. I may add that in the cases examined there was nothing to indicate that the *Anochetus* had appropriated *femoratus* nests.

3. Ule has given us no account of the growth or ontogeny of one of his ant-gardens based on actual observation. He implies that the ants either put seeds into crevices or accumulate a certain amount of humus at some spot on a tree or bush, especially at the junction of the branches, and then collect and plant the seeds in the mass. I feel confident that the gardens arise in a different manner. I occasionally found single ant epiphytes, especially *Peperomia* and one of the Gesneriaceae, growing in very small accumulations of earth or detritus in the crevices of tree-trunks or branches, and in many such cases no ants were present. In others incipient colonies of *Azteca, Crematogaster parabiotica* or *Camponotus femoratus* were found in similar situations, even about the roots of a single plant. I believe we have here one of the earliest stages in the development of the garden. That the amount of humus is gradually increased by the ants as the colony grows, admits of no doubt, and it is possible that as the accumulation becomes more voluminous, it may be seeded by seeds falling from the original plant. The frequent presence on a single nest of many plantlets of the same species and in approximately the same stage of growth may be as readily explained on this supposition as on that of the intentional garnering and sowing of seeds by the ants.

4. It is practically certain, from what we know of the habits of ants, that new gardens cannot be seeded from old ones, as Ule maintains. In Kartabo and its vicinity, the gardens are rarely close together. Once only did I find three strung along the trunk of a sapling only a few inches apart (Fig. 1). They are more frequently on different trees often separated by a hundred yards or more. Furthermore, the colonies of all the species of ants known

to inhabit the gardens, both in British Guiana and Brazil, are founded by single fecundated queens and not by division of the maternal colony, as Ule implies. There is little doubt that these single queens often start their colonies under the roots of epiphytes and that the earth for the garden is subsequently collected by her young colony of workers. And since the adult colonies of these various ants in British Guiana are found maturing and throwing off their sexual phases at a season when there is no fruit on the epiphytes, the planting of seeds by the nest-founding queens is out of the question.

5. I am skeptical in regard to the ability of some of the ants nesting in the gardens to collect seeds of the size mentioned by Ule. Seeds 4 mm. long, like those of the *Nidularium* could hardly be collected by such small ants as the Cremastogasters and Aztecas, and the *Anochetus* has mandibles of a shape peculiarly unsuited to collecting or carrying seeds of any kind. *Camponotus femoratus* would be the only species capable of doing such work, but in British Guiana, at least, the gardens inhabited by the ants of the three other genera have the same flora. Unfortunately Ule does not give the name of the ant used in his experiments. But even his experiments do not completely prove his point, owing to the fact that ants are so greedy and acquisitive that they will often carry all sorts of portable organic bodies into their nests, only to cast them out later when they find them useless.

6. Ule asserts that the ants not only sow the seeds in their gardens but actually cultivate ("pflegen") the growing plants. He records no convincing observations in support of this contention, and my own observations are purely negative. If he means more by his remarks than that the ants coat the rootlets with a soft earthen carton, modify their arrangement within the garden to suit their own convenience and prevent them from obstructing the galleries and chambers, I must remain skeptical till the details of the behavior of these insects have been more thoroughly studied.

I believe, therefore, that it is advisable at present to suspend judgment on the provenience and significance of the plant-elements in the ant-garden biocoenose of tropical America. Undoubtedly we have here problems of sufficient theoretical and economic importance to merit much closer scrutiny. For such investigations laboratories like the one maintained at Kartabo by the New York Zoological Society are admirably situated, but definite results will be secured only by those who can continue their observations and experiments over a much longer period than was possible for Ule and myself.

LITERATURE CITED

Emery, C.

'12 Family Formicidae, Subfamily Dolichoderinae in Wytsman's "Genera Insectorum." 137th fasc. 1912, 50 pp., 2 pls.

Forel, A.

'98 La Parabiose chez les Fourmis. Bull. Soc. Vaud. Sc. Nat. 34, 1898, pp. 380–384.

'04 In und mit Pflanzen lebende Ameisen aus dem Amazonas-Gebiet und Peru gesammelt von Herrn Ule. Zool. Jahrb. Abth. f. Syst. 20, 1904, pp. 677–707.

'12 Formicides Néotropiques. Part V. Mém. Soc. Ent. Belg. 20, 1912, pp. 33–58.

Mann, W. M.

'12 Parabiosis in Brazilian Ants. Psyche 19, 1912, pp. 36–41.

Ule, E.

'01 Ameisengärten im Amazonas-gebiet. Engler's Botan. Jahrb. 30, 1901, pp. 45–51, 1 pl.

'05 Wechselbeziehungen zwischen Ameisen und Pflanzen. Flora, 94, 1905, pp. 491–497.

'06 Ameisenpflanzen. Engler's Botan. Jahrb. 37, 1906, pp. 235–352, 2 pls.

Wasmann, E.

'15 Eine neue Pseudomyrma aus der Ochsenhorndornakazie in Mexiko. Tijdschr v. Ent. 58, 1915, pp. 296–325, 4 pls.

'15 Nachtrag zu "Eine neue Pseudomyrma aus der Ochsenhorndornakazie in Mexiko." Tijdschr. v. Ent. 58, 1915, Suppl. pp. 125–131.

Wheeler, W. M.

'01 The Compound and Mixed Nests of American Ants. Amer. Natural. 35, 1901, pp. 431–448, 513–539, 701–724, 791–818, 20 figs.

'13 Observations on the Central American Acacia Ants. Trans. Second Ent. Congr. Oxford (1912), 1913, pp. 109–139.